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BY

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(Contribution from West Virginia Agricultural Experiment Station)

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TRANSGRESSIVE SEGREGATION FOR SUSCEPTIBILITY TO SMUT IN AN OAT CROSS[1]

By R. J. GARBER, N. J. GIDDINGS, and M. M. HOOVER, *West Virginia Agricultural Experiment Station*

INTRODUCTION

In a recent paper [2] evidence of transgressive segregation for susceptibility to smut in the oat cross Gopher × Black Mesdag was presented. During the season of 1928 further data relative to this case were collected, and it is the purpose of the present paper to present some of these.

The pertinent literature was reviewed, and a description of the general methods followed in this investigation was given in the article cited above. During the season of 1928 the F_3 families were grown in triplicate plots, but the F_4 and F_5 families were grown in duplicate plots. In all, there were planted 120 seeds of each F_3 family, 80 seeds of each F_4 and F_5 family, and 40 seeds in each parental plot. The parents were interspersed at intervals of 10 plots (20 rows) among the progeny. Each plot in the nursery consisted of two rows 5 feet long. Consequently, with but 20 seeds planted per row, there was ample space for individual plant development.

All seed was treated with smut [3] spores about one month before the date of planting (June 16 and 18). A fairly successful smut epidemic was obtained, although in certain places in the nursery there seemed to be a somewhat lower infection than in others, as indicated by the degree of infection of the Gopher parent. Smut notes were taken after all the oats were completely headed and again at harvest time.

F_3 FAMILIES

The percentage of smutted plants and the color of seed of the F_3 families and of the parent stocks grown in 1928 as well as those already reported [4] are shown in Table 1. Of the 50 F_3 families grown in 1928, 13 showed no evidence of smut infection and 6 gave rather striking evidence of a susceptibility to smut greater than that of the Gopher parent. The other 31 F_3 families showed a range in percentage of smut infection which fell within that of the susceptible parent. It is apparent that the data collected in 1928 are similar to those obtained in 1926. In the latter year each F_3 family was grown in a single plot of three rows only, which accounts in part at least for the somewhat greater variability obtained. Each variate recorded in the frequency distributions for 1926 represents a single plot, whereas each variate recorded for 1928 represents triplicate

[1] Received for publication Feb. 19, 1929; issued December, 1929. Approved as Scientific Paper No. 72 by the director, West Virginia Agricultural Experiment Station.

[2] GARBER, R. J., GIDDINGS, N. J., and HOOVER, M. M. BREEDING FOR DISEASE RESISTANCE WITH PARTICULAR REFERENCE TO THE SMUT OF OATS. Sci. Agr. 9: 103–115. 1928.

[3] No effort was made to distinguish between loose smut (*Ustilago avenae*) and covered smut (*U. levis*), although most of the oat smut which occurs naturally in the vicinity of Morgantown, W. Va., is *U. avenae*

[4] GARBER, R. J., GIDDINGS, N. J., and HOOVER, M. M. Op. cit.

plots. On the basis of progeny tests it was found that 2 F_3 families recorded as "zero infection" in 1926 were wrongly classified. The correction has been made in Table 1.

Of the 150 F_3 families which were grown, 32 showed no evidence of smut infection and 13 showed transgressive segregation for smut susceptibility. Assuming that a single main factor difference is responsible for determining the high degree of resistance, if not immunity, of the Black Mesdag parent, one would expect one-fourth, or 37.5, of the F_3 families to be similar to it in smut reaction, whereas 32 actually were obtained. The difference (5.5 ± 3.6) is not significant.

TABLE 1.—*Number of smutted plants in various percentage classes and color of seed among the parents and F_3 families of an oat cross, Gopher × Black Mesdag, and the reciprocal, grown in 1926 and in 1928, at Morgantown, W. Va.*

Parent or progeny	Year grown	Color of seed	Number of plants in smut-percentage classes																Total
			0	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5		
Gopher	1926	White	1	1	1	1		3	2	1	1								11
Black Mesdag	1926	Black	11																11
F_3 families	1926	do	7	6	5	3		1	1			1		1				1	26
Do	1926	Segregating	7	8	19	9			2	2	1				3				51
Do	1926	White	5	6	1	4		2	1	1	2	1							23
Gopher	1928	do		2	2	1													5
Black Mesdag	1928	Black	5																5
F_3 families	1928	do	4	5	2	1		1											13
Do	1928	Segregating	7	6	7	1		2	2	1									26
Do	1928	White	2	2	6	1													11

The F_3 families which showed a susceptibility to smut greater than that of the Gopher parent indicate that at least one additional hereditary factor is conditioning smut reaction in this cross. The Gopher parent has consistently proved to be of moderate susceptibility as compared with the highly susceptible progeny lines.

LINKAGE

Some evidence of a genetic linkage between the black-color gene and at least one factor which is causing increased smut susceptibility has been published.[5] The data obtained in 1928 corroborate those obtained earlier. The six F_3 families which showed transgressive segregation for smut susceptibility were either black seeded or segregated for black-seed color. In 1926 there were also six F_3 families which showed susceptibility to smut clearly beyond the range of the Gopher parent and two additional families were doubtful but showed percentages of infection a little greater than that of the most susceptible plot of Gopher. One of these F_3 families had white seed and the other black.

F_4 FAMILIES

The F_4 families grown in 1927, and already reported, are shown in Table 2. Family 17–10–30 did not show any smut infection in F_3, but one of the five F_4 families grown from it had a single smutted plant. Further tests in F_5 indicated that this family was truly a

[5] GARBER, R. J., GIDDINGS, N. J., and HOOVER, M. M., Op. cit.

zero-infection strain; hence a correction has been made in the data originally published.

All of the families except one noted as zero infection in F_3 apparently bred true for this character in F_4. One F_3 family, 16–15–59, produced four F_4 families which showed smut to one which did not; consequently the F_3 should probably have been classed as a low-infection rather than as a zero-infection strain.

TABLE 2.—*Percentage of smutted plants among the F_3 families, number of smutted plants in various percentage classes among the respective F_4 families, and the parents grown among the latter, of an oat cross, Gopher×Black Mesdag, and the reciprocal, grown in 1927.*

Parent or progeny	F_3 families		Number of plants in various smut-percentage classes among F_4 families										Total [a]
	Plants	Smutted	0	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	
	Number	*Per cent*											
Gopher				3	7	5		1					16
Black Mesdag			16										16
16–15–4	64	0	5										5
16–15–8	66	1.5	3	1		1							5
16–15–7	64	12.5	1	3	1								5
16–15–39	60	55.0				2	2		1				5
16–15–16	70	0	5										5
16–15–31	66	1.5	2	3									5
16–15–1	51	13.7	2	1	2								5
16–15–21	70	27.1			3			1	1				5
16–15–17	70	0	8										8
16–15–35	63	0	5										5
16–15–36	54	20.4	2	1	1	1							5
16–15–53	69	0	5										5
16–15–55	70	27.1		1	1	1	1		1				5
16–15–59	65	0	1	3	1								5
16–15–64	60	0	5										5
16–15–68	73	28.8		2		3							5
17–10–1	68	0	5										5
17–10–21	65	56.9				2	1	1	1				5
17–10–22	65	1.5	1	2	1	1							5
17–10–35	65	27.7	1		1	2	1						5
17–10–30	61	0	5										5
17–10–54	63	11.1	3	1		1							5
17–10–62	67	0	5										5
17–10–64	67	50.7				2	1	1	1				5
17–10–52	70	0	5										5
17–10–68	55	65.5							1	2	1	1	5
17–10–53	68	0	5										5
17–10–75	71	57.7				1	2		2				5
17–10–72	65	1.5	2	1	2								5
17–10–48	65	0	10										10

[a] Most of the duplicated parental and F_4 plots contained from 65 to 70 plants. Thirty-two plots of each parent were grown, thus making 16 duplicates comparable to the F_4 families.

It is obvious from Table 2 that all the F_3 families classified as low-infection strains were heterozygous, as they produced both smutted and smut-free F_4 families. On the other hand, all the families which showed a high, and some of those which showed an intermediate degree, of smut infection in F_3 produced in F_4 only families which contained smutted plants.

In Table 3 are shown the F_4 families and the parents among them grown in 1928. The F_3 lines from which these F_4 families were derived were grown in the same year (1926) as the F_3 lines reported in Table 2.

There were eight F_3 lines noted as zero infection which were grown in F_4. All but one proved to be homozygous for this character. Strain 17–10–15 produced both smutted and smut-free F_4 families,

and hence probably should have been classed as a low-infection rather than as a zero-infection strain.

TABLE 3.—*Percentage of smutted plants among the F_3 families, number of smutted plants in various percentage classes among the respective F_4 families, and the parents grown among the latter, of an oat cross, Gopher×Black Mesdag, and the reciprocal, grown in 1928.*

Parent or progeny	F_3 families		Number of plants in various smut-percentage classes among F_4 families															Total
	Plants	Smutted	0	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	
	Number	*Per cent*																
Gopher				3	3	3												9
Black Mesdag			9															9
16–15–18	63	20.6	2	1	1	1												5
16–15–3	60	0	5															5
16–15–51	65	30.8							1			2		1	1			5
16–15–29	64	0	5															5
16–15–74	46	33.3						1	1	1				1		1		5
16–15–41	55	0	5															5
16–15–77	66	40.9				1					1		1	2				5
16–15–49	63	0	5															5
17–10–2	67	37.3			1	1	1	1	1									5
17–10–8	69	0	5															5
17–10–10	58	36.2					1		1	2	1							5
17–10–15	62	0	3	1		1												5
17–10–17	68	22.1							1	1	2			1				5
17–10–27	65	0	5															5
17–10–43	75	42.7						1	1	1	1			1				5
17–10–47	68	0	5															5
17–10–60	72	34.7			1			1		2			1					5
17–10–63	70	38.6					1	1			1			2				5

Strain 16–15–18 with an infection of 20.6 per cent smut in F_3 produced both smutted and smut-free F_4 families, whereas strain 17–10–17, with approximately the same degree of infection (22.1 per cent) in F_3, produced nothing but rather highly susceptible F_4 lines. The remaining eight strains, which ranged in smut infection from 30.8 to 42.7 per cent in F_3, produced only F_4 families which contained some smutted plants.

From the data reported it seems reasonable to conclude that the zero-infection F_3 lines are homozygous, that the low-infection F_3 lines are for the greater part heterozygous, and that the moderately high and the highly susceptible F_3 lines are probably homozygous for at least one main factor for susceptibility.

F_5 FAMILIES

The F_5 families and the parents grown among them in 1928, together with the ancestral F_4 lines grown in 1927, are shown in Table 4. In general, the F_5 lines derived from zero-infection F_4 families bred true to this condition. The exceptions were strains 16–15–31–1 and 16–15–53–3, each of which produced one F_5 family that contained a single smutted plant.

Family 16–15–8–5 contained 10.2 per cent smutted plants in 1927. From Table 2 it may be seen that three of the sibs of this family were recorded as zero infection, and one fell in the class of 2.5 per cent infection. The five F_5 families from line 16–15–8–5 (Table 4) fell into the following classes of percentage infection: One, zero; three, 2.5; and one, 12.5.

Family 16–15–7–5 was one of four sibs which showed a low percentage of smut infection in 1927. The other related F_4 line showed a zero percentage infection. In F_5, of the five descendant lines from 16–15–7–5, but one showed any smut and that one in a single plant only. Some of these lines may have been susceptible but escaped infection or, if infected, failed to give external evidence of it. A further test of these strains will be made in the F_6 generation.

TABLE 4.—*Percentage of smutted plants among the F_4 families, number of smutted plants in various percentage classes among the respective F_5 families, and the parents grown among the latter, of an oat cross, Gopher×Black Mesdag, and the reciprocal*

Parent or progeny	F_4 families		Number of plants in various smut-percentage classes among F_5 families							Total
	Plants	Smutted	0	2.5	7.5	12.5	17.5	22.5	27.5	
	Number	*Per cent*								
Gopher	------	------	2	4	5	3	------	------	------	14
Black Mesdag P	------	------	14	------	------	------	------	------	------	14
16–15–4–1	62	0	1	------	------	------	------	------	------	1
16–15–4–2	64	0	1	------	------	------	------	------	------	1
16–15–4–4	55	0	1	------	------	------	------	------	------	1
16–15–4–5	59	0	1	------	------	------	------	------	------	1
16–15–8–1	45	0	5	------	------	------	------	------	------	5
16–15–8–5	49	10.2	1	3	------	1	------	------	------	5
16–15–7–3	33	0	5	------	------	------	------	------	------	5
16–15–7–5	59	1.7	4	1	------	------	------	------	------	5
16–15–16–2	70	0	2	------	------	------	------	------	------	2
16–15–16–4	67	0	3	------	------	------	------	------	------	3
16–15–31–1	64	0	4	1	------	------	------	------	------	5
16–15–31–5	61	1.6	2	2	1	------	------	------	------	5
16–15–1–5	55	0	5	------	------	------	------	------	------	5
16–15–35–1	54	0	3	------	------	------	------	------	------	3
16–15–17–2	63	0	5	------	------	------	------	------	------	5
16–15–53–3	69	0	2	1	------	------	------	------	------	3
16–15–35–4	59	0	3	------	------	------	------	------	------	3
16–15–68–5	51	2.0	------	2	2	1	------	------	------	5
17–10–1–1	53	0	3	------	------	------	------	------	------	3
17–10–62–1	50	0	3	------	------	------	------	------	------	3
17–10–48–1	51	0	3	------	------	------	------	------	------	3
17–10–1–2	64	0	3	------	------	------	------	------	------	3
17–10–30–1	43	2.3	5	------	------	------	------	------	------	5
17–10–53–2	45	0	3	------	------	------	------	------	------	3
17–10–48–2	55	0	3	------	------	------	------	------	------	3
17–10–1–3	64	0	3	------	------	------	------	------	------	3
17–10–62–3	55	0	3	------	------	------	------	------	------	3
17–10–48–3	50	0	3	------	------	------	------	------	------	3
17–10–1–4	65	0	3	------	------	------	------	------	------	3
17–10–53–3	58	0	3	------	------	------	------	------	------	3
17–10–1–5	61	0	3	------	------	------	------	------	------	3
17–10–53–5	60	0	3	------	------	------	------	------	------	3
17–10–48–5	57	0	3	------	------	------	------	------	------	3
17–10–48–6	46	0	2	------	------	------	------	------	------	2
17–10–48–7	38	0	2	------	------	------	------	------	------	2
17–10–48–8	54	0	2	------	------	------	------	------	------	2
17–10–48–9	54	0	2	------	------	------	------	------	------	2
17–10–48–10	55	0	2	------	------	------	------	------	------	2
16–15–17–6	51	0	4	------	------	------	------	------	------	4
17–10–68–1	46	34.8	------	1	1	------	------	------	1	3
17–10–68–5	57	38.6	------	------	1	1	------	1	------	3
17–10–64–1	50	10.0	2	------	1	------	------	------	------	3
17–10–64–2	57	30.0	------	2	------	------	1	------	------	3

Line 16–15–31–5 is one of three F_4 families with the same ancestry that showed a low percentage of smut. The other two related F_4 families showed no smut. The F_5 descendants of 16–15–31–5 showed percentages of smut as follows: Two families with zero infection; two families which fell into the 2.5 per cent class; and one family into the 7.5 per cent class. In other words, these five F_5 families which descended from 16–15–31–5 reacted to smut in a manner very similar to that of the five F_4 families from 16–15–31.

Strain 16–15–68–5 was one of five F_4 lines with the same ancestry which showed a low percentage of smut infection. It is obvious from Table 4 that the five F_5 lines descended from this strain also showed a low percentage of smut infection, indicating homozygosity for the character.

In 1927 strain 17–10–30–1 was the only one of five F_4 families from the same F_3 line which showed any smut, and this strain showed smut in but a single plant. Although precaution was taken to prevent an accidental mixture, there is always the possibility of contamination from this source. Then, too, there is an appreciable amount of natural crossing in oats at Morgantown, as has been shown in a previous publication.[6] Whatever the cause of the single apparently susceptible plant observed in the F_4 family, none of the F_5 descendants showed any smut. The evidence strongly indicates that the F_3 line 17–10–30 was homozygous for the main factor controlling smut reaction.

Three F_5 families were grown from low-infection strain 17–10–64–1. Two of these showed no evidence of smut and one showed a percentage of smut that fell into the 7.5 class. This result was hardly expected, as F_4 strain 17–10–64–1 was one of five which showed smut. A further test in the F_6 generation will be made. This is of particular importance because of the fact that two of the duplicate plots of Gopher did not show any evidence of smut infection in 1928.

The three remaining F_4 strains which showed smut in 1927 and which were tested in F_5 were classed as moderately high in susceptibility. Each one of the three produced one F_5 family which showed a degree of smut infection greater than the most susceptible duplicate plots of Gopher.

PEDIGREES OF CERTAIN F_5 LINES

In order to bring some of the pedigrees together for comparison Table 5 has been prepared. It will be observed that all of the lines listed in the table which gave no evidence of smut infection in F_3 bred true for this condition through the F_5 generation. Two of the three F_3 families which showed a relatively low smut infection produced both infected and noninfected descendants. The third family, 16–15–31, produced three infected and two noninfected F_4 lines, and of the five F_5 families grown from one of the noninfected strains four showed no evidence of smut and one showed smut in a single plant only. The data seem to indicate the possibility that 16–15–31 also was heterozygous for smut reaction. Strain 16–15–68 contained 28.8 per cent smutted plants in F_3, a percentage well within the range exhibited by the Gopher parent grown the same year. The five F_4 families likewise showed percentages of smutted plants similar to Gopher grown that year, and again in F_5 the Gopher parent and the five families descended from one of the F_4 lines showed similar reaction, thus indicating that the genotypes of these lines are similar to that of one of the parents. The highly susceptible F_3 families, 17–10–64 and 17–10–68, produced only susceptible F_4 lines. The group from the former ranged from 10.0 to 29.8 per cent of smutted plants and from the latter 29.8 to 42.9 per cent. However, in F_5 two families descended from 17–10–64 and one from 17–10–68 gave

[6] GARBER, R. J., and QUISENBERRY, K. S. NATURAL CROSSING IN OATS AT MORGANTOWN, WEST VIRGINIA. Jour. Amer. Soc. Agron. 19: 191–197. 1927.

no evidence of infection. This fact may or may not be of genetic significance, particularly in view of the somewhat erratic smut epidemic obtained among the F_5 families. Further tests are being made. With the technic used in this experiment considerable variation in the percentages of smutted plants among the highly susceptible line was expected, but families without any smutted plants were not expected. It is evident from Table 5 that some of the F_5 families from the two highly susceptible F_3 lines again showed transgressive susceptibility.

TABLE 5.—*Pedigrees and number of smutted plants in various percentage classes among certain F_5 lines of the oat cross, Gopher × Black Mesdag, and the reciprocal*

Progeny	Smutted in F_3	Progeny	Smutted in F_4	Number of plants in various smut-percentage classes among F_5 families						
				0	2.5	7.5	12.5	17.5	22.5	27.5
	Per cent		*Per cent*							
16-15-7	12.5	16-15-7-3	0	5						
		16-15-7-5	1.7	4	1					
16-15-8	1.5	16-15-8-1	0	5						
		16-15-8-5	10.2	1	3		1			
16-15-16	0	16-15-16-2	0	2						
		16-15-16-4	0	3						
16-15-17	0	16-15-17-2	0	5						
		16-15-17-6	0	4						
16-15-31	1.5	16-15-31-1	0	4	1					
		16-15-31-5	1.6	2	2	1				
16-15-35	0	16-15-35-1	0	3						
		16-15-35-4	0	3						
16-15-68	28.8	16-15-68-5	2.0		2	2	1			
17-10-1	0	17-10-1-1	0	3						
		17-10-1-2	0	3						
		17-10-1-3	0	3						
		17-10-1-4	0	3						
		17-10-1-5	0	3						
17-10-48	0	17-10-48-1	0	3						
		17-10-48-2	0	3						
		17-10-48-3	0	3						
		17-10-48-5	0	3						
		17-10-48-6	0	2						
		17-10-48-7	0	2						
		17-10-48-8	0	2						
		18-10-48-9	0	2						
		18-10-48-10	0	2						
17-10-53	0	17-10-53-2	0	3						
		17-10-53-3	0	3						
		17-10-53-5	0	3						
17-10-62	0	17-10-62-1	0	3						
		17-10-62-3	0	3						
17-10-64	50.7	17-10-64-1	10.6	2		1				
		17-10-64-2	30.0		2			1		
17-10-68	65.5	17-10-68-1	34.8	1		1				1
		17-10-68-5	38.6			1	1		1	

INHERITANCE OF SMUT REACTION

A considerable number of F_1 plants have been grown in connection with this investigation, but even though the crossed seed was treated with smut spores no smutted F_1 plants have been found. In 1928 some crossed seed was hulled, treated with smut, and then planted. Of the 23 plants produced, none showed any evidence of infection. Resistance apparently behaved as a dominant in the cross Gopher × Black Mesdag and the reciprocal.

In considering the inheritance of smut reaction it may be well first to reexamine the 100 F_3 families grown in 1926, when a severe

epidemic was obtained, and take into account the behavior of the F_4 generation. To aid in this reexamination Table 6 has been prepared. A family was considered as segregating if it produced both infected and noninfected descendant lines. Of course this classification does not take into account families which may be segregating for degree of susceptibility.

TABLE 6.—*Breeding behavior of certain F_3 families as revealed in the F_4 generation of an oat cross, Gopher × Black Mesdag, and the reciprocal*

Smut percentage class in F_3	Breeding nature of F_3 plants as shown in F_4	F_3 families
		Number
0	Homogynous resistant	19
	Segregating	2
0.1–9.9	do	4
10 –19.9	do	3
20 –29.9	Homogynous susceptible	4
	Segregating	3
30	Homogynous susceptible	13

It is apparent from Table 6 that of the 21 F_3 families which showed no smut, 19 bred true to this condition in F_4. In all cases at least 5 F_4 families were grown from each F_3 line that was tested. The 2 F_3 lines which segregated in F_4 should have been classified as low-infection strains. The 7 F_3 families which showed a percentage of smut infection between 0 and 19.9 segregated in the next generation, and of the 7 F_3 lines with a percentage of smutted plants from 20 to 29.9, inclusive, 4 bred true and 3 segregated. All of the 13 F_3 lines with a percentage of smutted plants 30 or above bred true. In view of this situation, the 100 F_3 families grown in 1926 (Table 1) may be classified as follows: Nineteen bred true for zero infection; 64 segregated and 17 bred true for more or less infection, a ratio which departs rather significantly from monohybrid expectation (P = approximately 0.03 with 2 degrees of freedom [7]). If the segregating families and those which bred true for more or less infection are grouped together, the deviation (6.0 ± 2.9) is hardly significant.

It will be observed from Table 6 that only seven F_3 families which showed percentages of smutted plants between 0.1 and 19.9 were tested in F_4. It is possible that if more families in this F_3 group had been grown, a few homozygous ones would have been found. Moreover, it should be pointed out that a few F_2 plants, from which the F_3 lines were derived, were eliminated because they were infected with smut and produced little if any seed. One or both of these causes may have been instrumental in producing the departure from expectation noted above.

Considering the 50 F_3 families grown in triplicate plots in 1928 (Table 1) and placing them in two classes, those which showed no smutted plants and those which did, a ratio of 13 to 37, respectively, is obtained; a very close agreement with a 1:3 ratio. It seems reasonable to conclude that one main factor difference was operative in determining the resistance or immunity of the Black Mesdag parent in this cross.

[7] FISHER, R. A. STATISTICAL METHODS FOR RESEARCH WORKERS. 239 p., illus. London. 1925.

The data collected from the F_5 generation for the most part bore out the conclusion just stated. Some irregularities did appear, but they may have been due to nongenetic causes. Further tests are being made in the F_6 generation.

TRANSGRESSIVE SEGREGATION

Families were obtained in the F_3 and later generations which contained a distinctly greater percentage of smutted plants than did the susceptible parent grown in close proximity, thus indicating that transgressive segregation had taken place. It seems probable that the Black Mesdag parent brought into the cross one or more factors which increased susceptibility when associated with the susceptibility factor of Gopher. The results obtained thus far may be explained fairly satisfactorily by assuming that Black Mesdag carries a dominant factor (*R*) which gives high resistance, if not actual immunity, and another factor (*i*) which when associated with the homozygous condition for susceptibility (*r*) of the Gopher parent results in transgressive segregation. The reaction of Gopher to smut suggests that the *I* factor carried by it may act as an inhibitor to *r* or that it is an additional factor for resistance but less potent than the *R* factor carried by Black Mesdag.

A tentative factorial analysis follows:

Parents:	F_3	F_4
Black Mesdag, *R R i i*.	*R R I I*	
Gopher, *r r I I*.	2 *R R I i*	Breed true for resistance.
	R R i i	
	2 *R r I I*	
	4 *R r I i*	Low susceptibility and segregate in F_4.
	2 *R r i i*	
	r r I I	Breed true for susceptibility of Gopher.
	2 *r r I i*	Somewhat more susceptible than Gopher.
	r r i i	Breed true for high susceptibility.

On the basis of this hypothesis approximately one-sixteenth, or 9.4, of the 150 F_3 families would be expected to show transgressive susceptibility. There were 13 such families actually obtained, i. e., families which showed percentages of smutted plants greater than the most susceptible plots of the Gopher parent. The departure from expectation is 3.6 ± 2.

The F_3 families homozygous for *R* (should) breed true for zero infection, and for the most part such results were actually obtained. The F_3 families from F_2 plants heterozygous for *R* (should) show low susceptibility similar to Gopher, but (should) show segregation in the F_4 generation. The seven F_3 families which showed a low infection and the two additional F_3 families which did not show any smutted plants, but probably should have been classified as low-infection strains, all segregated in F_4. Of the seven F_3 families which showed percentages of smutted plants from 20 to 29.9, inclusive, four segregated and three showed some smutted plants, but only one (16–15–68) of this latter group apparently bred true for the degree of susceptibility of the Gopher parent. On the basis of the above hypothesis about one-ninth of the slightly susceptible F_3 strains would be expected to breed true.

Mention already has been made of the fact that the black-color gene *B* of the Mesdag parent seems to be linked with the *i* factor. Certain back crosses have been made, and it is hoped that the data obtained from these will not only clear up this linkage relation, but will also clarify the inheritance situation.

SUMMARY AND CONCLUSIONS

Gopher, a pure-line selection of oats moderately susceptible to smut, was crossed with a highly resistant if not immune pure-line selection of Black Mesdag. The inheritance of resistance to smut in relation to seed color has been studied through the F_5 generation.

Resistance to smut is apparently dominant and controlled by a single main factor difference. Evidence of a modifying factor or group of factors was also obtained. Certain lines descendant from the cross showed distinctly greater susceptibility to smut than did the Gopher parent grown at the same time.

There is apparently a linkage between the black-color gene and a modifying factor which is bringing about transgressive segregation for susceptibility.

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